Feeding Preferences in a Population of the Land Snail *Helminthoglypta arrosa* (Binney)

(Pulmonata : Helicidae)

BY

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INTRODUCTION

The determination of feeding preferences, frequently an important factor in understanding the ecology of animals has been undertaken for a wide variety of pulmonates. Additional information on land snail and slug food preferences has come from plant palatability studies (see discussion below for references).

I report here the feeding preferences of the land snail *Helminthoglypta arrosa* (Binney, 1855) for potential foods occurring in a lupine scrub stand (*Lupinus arboreus* Sims) on Mussel Point, Bodega Head, Sonoma County, California (38°20′N, 123°04′W, about 104 km north of San Francisco). In addition I compare my results with those reported for other pulmonates and examine the implications and applicability of plant palatability studies for terrestrial snails and slugs.

MATERIALS and METHODS

During my study *Helminthoglypta* was never observed eating living or dead animal matter; therefore I concentrated my attention on plant matter as possible food for this snail. Evidence that *Helminthoglypta* consumed a particular plant type was provided: (1) by observing snails in both field and laboratory throughout the snail's diurnal cycle approximately every 3 weeks between March, 1966 and June, 1967 and at least semiweekly from June 1967 to December, 1969; (2) by finding grazing damage on the plants; and (3) by examining the feces, for the color of materials in the fecal strings was practically unchanged from ingestion to egestion [this phenomenon has been observed for other pulmonates (Lowell L. Getz, personal communication, and Grime *et al.*, 1968) and is a phenomenon that has been used in the "marker food" technique in phalangid studies (Phillipson, 1960)].

The purpose of Series I laboratory experiments was to confirm field observations of acceptance or rejection of specific plants as food. Snails, which ranged in age from young-of-the-year to adults, were confined from 1 to 3 days in a moist and cool environment with freshly collected living and dead samples of plant species that commonly occurred in the lupine scrub stand. Prior to the presentation of a plant sample, snails had no plant material left over in their digestive tracts from previous feedings: I fed *Helminthoglypta* wet paper towels, and when snail fecal strings contained nothing but toweling, I assumed the snail's guts contained only toweling. At that point I presented the plant samples to snails.

In series II laboratory experiments I determined feeding preferences for the plants which were found acceptable as food in the field observations and in Series I. In a number of trials (see Table 2) I placed varying numbers (9 to 48, see Table 2) of snails of all sizes in the center of the floor of a cylindrical chamber (100 cm diameter by 50 cm). Equal wet weights of the different accepted plant samples were placed at least 10 cm apart on the periphery of the cylinder floor. The snails, floor, and plants were uniformly wetted at the start of each trial.

At the end of each trial (ca. 12 hrs), I recorded (1) the plants on which snails were found crawling, (2) any grazing damage, and (3) the color of the fecal strings. I assumed that when snails were found crawling on a particular plant type, they had been eating that plant. This assumption was corroborated by grazing damage on the plants in question and by the presence of feces the same color as the plants on which the snails had been found crawling. The relative positions of the plants were changed for each trial and the floor of the chamber was scrubbed between trials.

Series II experiments were conducted (1) twice in late spring and early summer (1968), when numerous green plants were available for testing, (2) once in mid-autumn (1968), when mostly dead plants were available, and (3) twice in winter (1969), when both green and dead specimens of the same plant species were available. No trials were conducted from mid-summer to early autumn, since all snails were generally in aestivation at that time (van der Laan, 1975).

RESULTS

From the field observations and the Series I experiments (Table 1) I learned that *Helminthoglypta* rejected all grasses, a fern, a bush, and 7 forb species. The accepted plants included 7 vascular species and a bracket fungus (Table 1). The fungus was so rare that its presence was never recorded in over 800 random plant cover samples (van der Laan, 1971). Thus it probably was not an important component of *Helminthoglypta*'s diet and consequently was not included in the Series II experiments. As far as I could observe, the bracket fungus was the only fungus used for food by *Helminthoglypta*. No grazing damage was evident on any other mushrooms or puffballs. I cannot however dismiss the possibility that *Helminthoglypta*, like other pulmonates (see discussion below), derived nutrition from other fungi in the soil or in the leaf litter. This fungal material was too small and indistinguishable to detect in snail feces. It also was suggested to me (Heinz, Wandelt, personal communications) that the snails might eat the green algae that grow on the woody parts of *Lupinus*, but green color never appeared in any snail feces after the snails were presented lupines which had algae on them. In addition, fecal material that I examined from snails during the autumn and early winter, when algae were abundant, contained no green color.

The Series II experiments conducted in late spring and early summer showed that snails had no preference for any particular green plant (the distribution of snails observed on the various plants was not significantly different from a uniform distribution; Table 2). During the autumn and first winter Series II experiments the snails showed a striking preference for dead over green plants (the observed distribution was significantly different from a uniform distribution, $p < 0.0001$; Table 2). This preference was still manifest in the second winter experiment, but at this time there appeared to be somewhat of a switch to green food (the observed distribution differed significantly from a uniform distribution, $p < 0.05$; Table 2).

The Series II experiments also showed that snails of all sizes have the same food preferences. There were no significant differences (using X^2) between snail size and kind of food selected. In the only other pulmonate study I know of (Frömming, 1954: 257; table 55) both quantitative and qualitative diet differences were noted when comparing juveniles with adults.

DISCUSSION

The habits of herbivory and saprophagy found for *Helminthoglypta* agree with most previous studies of pulmonates. Land snails are able to digest cellulose, according to Morton (1960), who has stated that most pulmonates are herbivores and believed that land snails and slugs have a "prolific supply of plant food," especially decaying plant material. Both Franc (1968) and Pelseneer (1935), after extensive reviews of the literature, concluded that the great majority of pulmonates are herbivores [a few pulmonates feed on animal matter; for example, Frömming, 1954, and Mason, 1970, reported *Oxychilus* feeding on earthworms and other snails; *Haplotrema* preys on other snails (Ingram, 1942) and *Deroceras agreste* Linnaeus was noted feeding on a recently dead sowbug *Armadillidium vulgare* (Ingram, 1946a)]. Pelseneer (*op. cit.*) and Fröming (*op. cit.*) mentioned a number of snail species that, like *Helminthoglypta*, feed on fungi; however, unlike *Helminthoglypta*, macroscopic fungi (mushrooms and puffballs) make up a major portion of the species' diets. Boycott (1934) and Gain (1891) stated for land mollusks in Great Britain the normal food (as for *Helminthoglypta*) consists of the decayed remains of the higher plants and fungi. In addition, the British Pulmonata (unlike *Helminthoglypta*) eat lichens and algae. Boycott also reported that pulmonates would eat partly digested vegetable remains in rabbit and sheep dung. The coprophagous habit was also observed with slugs on human feces in the hills above Oakland, California (C. Hand, personal communication). I have observed *Ariolimax columbianus* (Gould, 1851), the giant western slug, feeding on deer scat. I occasionally observed *Helminthoglypta* near rabbit and deer droppings, but I never observed my snail feeding on dung.

Not only do pulmonates as a group eat a wide variety of foods, but individual species have been shown to be catholic in their choice of plant foods. Three species of slugs in England "accepted a wide range of food," ac-

Table 1

The plant species from Bodega Head, Sonoma County, California, which were rejected or accepted as food by *Helminthoglypta arrosa* as noted in field observations and Series I (see text) laboratory experiments.

Accepted

Amsinckia Menziesii (Lehmann) Nelson & Macbride
Amsinckia spectabilis F. & M.
Phacelia distans Bentham
Montia perfoliata (Donn) Howell
Stellaria media (Linnaeus) Cyrillo
Silene gallica Linnaeus
Cardamine oligosperma Nuttall
Basidiomycete (Bracket fungus)

Rejected

Pteridium aquilinum (Linnaeus) Kuhn
Rumex acetosella Linnaeus
Stachys rigida Nuttall *ex* Bentham
Marah fabaceus (Naudin) Greene
Chenopodium californicum (Watson) Watson
Lupinus arboreus Sims
Solanum sp
Sonchus sp
Silybum Marianum
Graminae
Basidiomycete (mushrooms and puffballs)
Alga (on bark of *Lupinus*)

cording to Hunter (1968). This includes both green and dead plant material. Indeed the range of food can be quite wide as indicated by the fact that *Helminthoglypta* from Bodega Head, *Cepaea nemoralis* (Linnaeus, 1758) from England (Grime *et al.*, 1968), and *Caracollus carocolla* from Puerto Rico (Heatwole, 1965) eat paper towels and filter paper.

Even though diets are broadly based, pulmonates have definite food preferences as demonstrated in my study (Table 1) and in studies of others (Dall, 1913; Frömming, 1954; Grime *et al.*, 1968; Grime & Blythe, 1969; Ingram, 1946b; Ingram & Hand, 1949; Ingram & Peterson, 1947; Mason, 1970). An exhaustive analysis of differences and similarities in pulmonate diets is beyond the scope of this paper. It appears however that, as would be expected, closely related snail species have more similar diets than more distantly related species (see for example Frömming, 1954: 63; table 6; and p. 108; table 15). Variation in preference for a particular plant genus or species occurs. For example, *Rumex* was rejected by *Helminthoglypta* (Table 1) and *Lacinaria* and accepted by *Succinea* and *Retinella* (Frömming, 1954). On the other hand, it appears that food preferences for a particular plant species and genus were quite similar and that preferences for particular plant families varied more. Recall that *Helminthoglypta* accepted *Montia perfoliata* (Donn) Howell and *Stellaria media* (Linnaeus) Cyrillo (Table 1), plants which were preferred by *Ariolimax* (Ingram & Peterson, 1947). Similarly, *Stachys*, a mint, was rejected by *Helminthoglypta* (Table 1), "nibbled at" by *Ariolimax* (Ingram & Petersen, *op. cit.*), and only eaten when dead by *Zonitoides* (Frömming, *op. cit.*). *Lupinus*, a legume rejected by *Helminthoglypta* (Table 1), was also rejected or only nibbled at by *Zonitoides* (Frömming, *op. cit.*). On the other hand, other Leguminosae were preferred by *Helix aspersa* Müller, 1776 (Ingram, 1946b). All Graminae were found to be unpalatable to *Ariolimax* (Ingram & Petersen, *op. cit.*) (like *Helminthoglypta*), and with the exception of one graminoid species, all fresh grasses were rejected by *Cepaea* (Grime *et al.*, *op. cit.*; Grime & Blythe, *op. cit.*). On the other hand, unlike *Helminthoglypta*, *Cepaea* ate "senescent" grass blades.

Similar food preferences and wide ranging diets imply that nutritional needs are quite similar throughout the Pulmonata. Information on nutrition would be helpful in understanding diets, but unfortunately there is an extreme paucity of such data for mollusks (Gardiner, 1972). Fortunately, plant palatability, the other half of the pulmonate-plant relationship, has been examined, which sheds some light on feeding preferences and leads to some interesting ecological implications for snails and slugs.

Grime and his co-workers (1968, 1969) suggested that plants have evolved solutes which act as "chemical" attractants or deterrents to pulmonate feeding. In line with this theory I note that *Helminthoglypta* and *Zonitoides* (see above) rejected *Lupinus* which has a high alkaloid concentration; that *Helminthoglypta* and *Lacinaria* (see above) rejected *Rumex* which has a high oxalic acid concentration; and that my snail (Table 1) and many pulmonates in Europe (Frömming, 1954) rejected the nightshade *Solanum*. In addition, *Helminthoglypta* accepted no plants with known high concentrations of toxins. On the other hand, knowing that a plant is toxic for human beings or range animals does not imply that that plant will be toxic or repellent for pulmonates, for Frömming (*op. cit.*) has found snails and slugs eating and sometimes completely consuming plants toxic for mammals: *Amanita, Russula, Datura, Nicotiana,* and *Cannabis.*

Grime and co-workers also concluded that plants with hard exteriors are rejected. With respect to plants on Bodega Head, hard exteriors are characteristic of *Pteridium, Marah, Chenopodium*, and the grasses, all rejected by *Helminthoglypta.* On the other hand, the preferred

Table 2

Food preferences made by *Helminthoglypta arrosa* in Series II laboratory experiments.
Plant samples were green at the time of experiment unless noted as dead.

Inclusive Dates of Experiments	Number of Trials	Plant Species Presented	Number of Snails Observed	Number of Snails Expected
31 May, 1968	14	*Montia perfoliata*	36	30.7
to		*Amsinckia* spp.	33	30.7
16 July, 1968		*Stellaria media*	28	30.7
Late Spring		*Phacelia distans*	20	30.7
Early Summer		*Silene gallica*[1]	37	30.7
Chi-square = 6.18 (Not significant)				
31 May, 1968	3	*Montia perfoliata*	9	7.2
to		*Amsinckia* spp.	11	7.2
14 June, 1968		*Stellaria media*	6	7.2
Late Spring		*Phacelia distans*	6	7.2
		Silene gallica	3	7.2
		Cardamine oligosperma	8	7.2
Chi-square = 5.42 (Not significant)				
29 Oct. 1968	5	*Phacelia distans*	6	17.7
to		*Phacelia distans* Dead	29	17.7
2 Nov. 1968		*Silene gallica* Dead	18	17.7
Mid-Autumn				
Chi-square = 14.95, $p > 0.0001$				
29 Jan. 1969	3	*Montia perfoliata*	1	3.2
to		*Stellaria media*	0	3.2
30 Jan. 1969		*Phacelia distans*	0	3.2
Winter		*Phacelia distans* Dead mixed with *Amsinckia* spp. Dead	12	3.2
Chi-square = 31.62, $p > 0.0001$				
27 Feb. 1969	2	*Montia perfoliata*	3	7.2
to		*Stellaria media*	3	7.2
28 Feb. 1969		*Cardamine oligosperma*	8	7.2
		Phacelia distans	9	7.2
Mid-winter		*Phacelia distans* Dead mixed with *Amsinkia* spp. Dead	13	7.2
Chi-square = 10.11, $p > 0.05$				

[1] *Silene gallica* was presented in 13 trials only during this time period. A correction (14/13) of the number of snails observed was made.

plants *Stellaria, Silene,* and *Amsinckia* have hard exteriors. By contrast, *Montia, Phacelia, Cardamine* and dead *Amsinckia* have outer surfaces that were easily broken by snail grazing. *Lupinus* also has leaves with soft exteriors, which, recall again, was rejected by *Helminthoglypta*; however, the lupine's high alkaloid concentration was probably more important in the rejection than leaf texture.

Robert Browning[1] notwithstanding, Grime (personal communication) additionally proposed that the selection of spiny plants for food by terrestrial pulmonates was exceptional. He found that *Cepaea* did not seem able to maintain adherence and traction on *Urtica dioeca*, which is chemically attractive to the snail, but which is spiny.

I have never observed *Helminthoglypta* crawling on the leaves or stems of any of the spiny thistles *Sonchus* sp. and *Silybum marianum* (Linnaeus) Gaertner that grew on Bodega Head, which is consistent with Grime's suggestion. In addition, recall that *Helminthoglypta* rejected and *Ariolimax* showed low interest in *Stachys*, which is a spiny plant. On the other hand, *Helminthoglypta* preferred, especially dead, *Amsinckia* (Tables 1 and 2), which is a very spiny plant. *Amsinckia*, unlike *Sonchus, Silybum*, and *Stachys*, grew prostrate on Bodega Head; therefore snails did not need to climb them. Thus spines *per se* probably are not sufficient to stop pulmonate feeding, but they may be critical on upright plants where snails must adhere to stems.

In an additional study using the slugs *Arion* and *Ariolimax* ORIANS & CATES (University of Washington, Seattle, unpublished data) found that early successional plants, especially annuals and biennials, were generally more palatable than late successional plants with high altitude plants intermediate in palatability.

Based on Orians and Cates' results I suggest that the following speculations should be examined by students of terrestrial mollusks: (1) Greater volume and variety of palatable food should tend to make molluscan abundance and species diversity highest in early successional plant communities. (2) Terrestrial gastropods in more mature plant communities should aggregate in disturbed areas where annuals, biennials and early successional plants temporarily grow. (3) Finally, in mature versus young communities snails and slugs, finding a higher frequency of unpalatable plants, will tend more to saprophagy, for upon plant death palatability will increase since feeding deterrents will be reduced: plants become prostrate, spines and hard exteriors decompose and "chemical" deterrents are leached.

SUMMARY

Helminthoglypta arrosa, like most terrestrial pulmonates, acts as an herbivore and reducer of dead plant material, accepting as food 7 forb species and 1 bracket fungus and rejecting 9 forbs, all grasses, an alga and all other macroscopic fungi. Dead plant material was strongly preferred over living material; no preferences were found among the acceptable plant species. Size of snails was not related to variation in diet preferences.

Helminthoglypta is similar to other land mollusks in accepting a wide range of food. Similarities and differences in feeding preferences between terrestrial pulmonates appear to be closely related to plant phylogenetic affinities, which indicates a similarity in nutritional needs throughout the Pulmonata and emphasizes the importance of evolution of plant palatability. Previous observations of *Cepaea* (GRIME and co-workers, 1968, 1969) suggested that plants deterred feeding by evolving "chemical" deterrents, hard exteriors and spines. *Helminthoglypta* avoided 2 species with "chemical" deterrents and accepted no plants with known high concentrations of toxins. The snail both rejected and accepted plants with hard exteriors and spines. Spines appear to be critical only on upright plants where snails must adhere to stems in order to feed.

Based on previous findings (CATES & ORIANS, 1974) that the frequency of palatable plant species is inversely related to the maturity of the plant community, I suggest here that in late as compared to early successional communities snails and slugs will tend to have lower abundances and lower species diversity, tend to select disturbed areas more often for feeding, and tend to saprophagy more than herbivory.

ACKNOWLEDGMENTS

This work forms part of a Ph. D. dissertation supported in part by a pre-doctoral fellowship #5 FO1 GM36483-03 from the National Institutes of Health and presented at the University of California, Berkeley. I wish to thank Oscar H. Paris and Carrie van der Laan for providing considerable support and advice and thank Kenneth Hagen, Frank A. Pitelka, Howell V. Daly, Rosalind Ribnick and Thums Fooman, Jr. for reviewing earlier versions of this manuscript. I am grateful also for the logistic support of

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[1] "The lark's on the wing;
The snail's on the thorn;
God's in his heaven --
All's right with the world."
(R. Browning, Pippa Passes, Part I [italics mine])

the director, Cadet Hand, students and staff of the Bodega Marine Laboratory. Special thanks are due Gordon Orians and Rex Cates for sharing unpublished data.

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